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Life History and Productivity of the Phoxocephalid Amphipod 'Rhepoxynius abronius' (Barnard)

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LIFE HISTORY AND PRODUCTIVITY OF THE PHOXOCEPHALID AMPHIPOD *RHEPOXYNIUS ABRONIUS* (BARNARD)

Paul F. Kemp, Faith A. Cole, and Richard C. Swartz

ABSTRACT

Rhepoxynius abronius (Barnard) (Amphipoda: Phoxocephalidae) is a predominantly subtidal species of the North American Pacific coast. It is also found sub- and intertidally within the polyhaline region of estuaries of Oregon and Washington. Within the Yaquina Bay estuary, Oregon, *R. abronius* is an annual species producing one or two broods per year. Recruitment occurs over an extended period from mid to late winter through summer. Mortality was 20–25% per month during mid to late spring through fall, and was low in winter through early spring. Mortality may be largely due to predation. Mortality of males appears higher than that of females during the reproductive season. The annual range in biomass was 40–180 mg ash-free dry weight (AFDW)/0.5 m^2, averaging 104 mg AFDW/0.5 m^2. Secondary production was 160–216 mg AFDW/0.5 m^2/yr and the annual ratio of production to mean biomass was 1.54–2.08. Production and the production : biomass ratio are similar to values reported for other marine amphipods with one or fewer generations per year.

Phoxocephalid amphipods are a widely distributed group of crustaceans characteristically inhabiting sub- and intertidal sandy sediment (Bousfield, 1973). They are among numerically dominant species in nearshore sediment of the North American west coast (Oliver *et al.*, 1980). Formerly considered detritivores (Enequist, 1949), some phoxocephalids are effective predators of larval polychaetes and may be important in regulating benthic community structure (Oliver *et al.*, 1982; Oakden, 1984). They are also significant in the diet of commercially exploited fish species (Ambrose, 1976; Van Blaricom, 1978). Despite their abundance and potential importance as both predators and prey in benthic communities, little is known of the life histories and productivity of phoxocephalid amphipods. The life history of *Rhepoxynius abronius* (Barnard) was studied through quarterly sampling of a California outer coastal population (Hannan *et al.*, 1979). Some life history data are also available for *Rhepoxynius fatigans* (Hannan *et al.*, 1979). The production biology of the phoxocephalid *Harpinia propinqua* has recently been studied (Wildish, 1984).

Abundant populations of *Rhepoxynius abronius* occur within Oregon and Washington estuaries under environmental conditions differing from those experienced by outer coast populations. These estuarine populations are the source of specimens used in experimental bioassays of sediment toxicity (Swartz *et al.*, 1979, 1982, 1984, 1985). Because of the practical and ecological importance of *R. abronius*, we have conducted a one-year study of the life history and productivity of this species in the Yaquina Bay estuary, Oregon.

METHODS

Collections

The study site is an apparently uniform sandy bottom area adjacent to the central dredged channel of Yaquina Bay (44°37.6′N, 124°3.0′W), with an average depth of 5 m below mean lower low water. Its approximate dimensions are 50 by 100 m. Depth varies by less than 2 m. Sediment is well-sorted

fine sand with less than 2% organic content (weight loss at 550°C). Near-bottom salinities measured during collections varied from 22‰ to 33‰, and were usually above 27‰. The lower salinities were found when increased precipitation occurred in winter. Water temperatures varied from 8°C to 13°C with a decrease in winter, but minimum temperatures occurred in summer during seasonal nearshore upwelling. Benthic samples were obtained with a 0.05-m^2 Smith-McIntyre grab at monthly intervals from 11 March 1980 to 10 July 1980. Sampling frequency from 10 July 1980 through 5 March 1981 was increased to every 2 weeks to detect short-term changes in abundance. A preliminary sample of 5 grabs collected on 6 February 1980 was used to evaluate the sieving and sampling procedures. Thereafter, 10 replicate grabs were taken for each sample and all densities are based on a total sample area of 0.5 m^2. Grab samples were returned to the laboratory and sieved through nested 1.0 and 0.5-mm screens. No additional *Rhepoxynius abronius* juveniles were recovered when a 0.25-mm screen was used to resieve sediment passing the 0.5-mm screen. Material retained on each screen was preserved in 10% buffered formalin and transferred to 70% ethanol prior to examination.

Measurement, Enumeration, and Classification

Specimens were examined under a dissecting microscope equipped with a calibrated ocular micrometer. Amphipods were straightened with forceps and their length was measured to the nearest 0.1 mm as the distance from the posterior edge of the head to the posterior edge of the third pleonite. The head and posterior abdomen (i.e., urosome) were excluded from length measurements because they are strongly flexed in preserved specimens. Specimens were later grouped into 0.3-mm size classes. Individuals were classified as sexually mature, immature, or juvenile. Mature males were defined as having copulatory papillae, elongated second antennae, and enlarged eyes. Immature males lacked at least one of these characters. Males nearing maturity were not distinguished from fully mature males. Mature females included ovigerous and nonovigerous specimens. Nonovigerous mature females had fully developed, setose oostegites but no eggs or young. Immature females had oostegites lacking setae. Immature males and females could always be reliably discriminated at sizes ≥ 2.7 mm. Juveniles lacked discernible sexual characteristics. Contents of the brood pouches of ovigerous females were removed and counted. Egg size and egg developmental stage were not recorded, except that broods that appeared ready to emerge were noted.

Prior to 10 July 1980, all specimens were measured and counted but only mature male and ovigerous female classes were identified. After 10 July, all specimens retained on the 1.0-mm screen were classified, measured, and counted. The 0.5-mm screen fractions of replicate grab samples were selected in random order for examination. If the total number of individuals retained on the 0.5-mm screen in 10 grabs exceeded 200, at least 3 of the 10 grabs, containing a minimum of 200 individuals, were fully examined. The remaining individuals in the 10 grabs were counted and size-frequency data for the entire 0.5-mm screen fraction were extrapolated from the subsample.

Data for the 10 grabs were pooled for estimates of abundance, fecundity, mean size, and for the length–frequency histograms. The coefficient of variation for the number of individuals per grab, calculated for each set of 10 grabs and averaged over all sets, was 46.4%.

Biomass Estimation

Biomass was estimated using a weight-length conversion equation. Groups of 4–10 freshly collected amphipods in each of ten 0.3-mm length classes were weighed wet (blotted on tissue paper), after drying for 4 h at 70°C, and after ashing for 4 h at 550°C. The resultant weight-length data were fitted by a power function of the form: $\text{weight} = a(\text{length})^b$, by least squares regression of log-transformed data.

Results

Size Frequency Histograms

Most individuals collected on 6 February 1980 were ≥ 2.4 mm in length. Increasing numbers of small individuals were obtained in subsequent sampling (Fig. 1). These were similar in size to fully developed young in the brood pouch (0.8–0.9 mm) and represent recently released young-of-the-year. With increasing numbers of these recruits, the size-frequency distribution became strongly bimodal from 11 March to 9 May 1980, after which the two size modes merged. The distribution remained dominated by small individuals through September 1980. During October through mid-January, relatively few small individuals were found and the size distribution became progressively less skewed. The size distribution

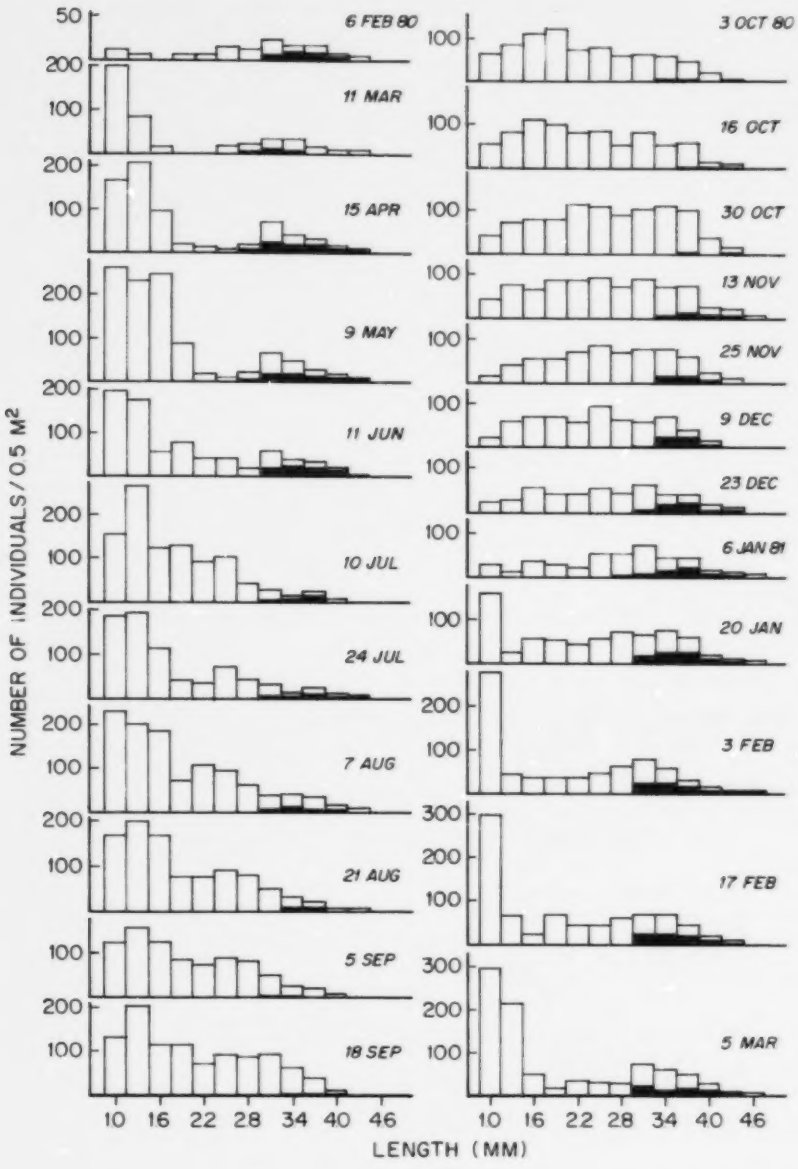

Fig. 1. Length–frequency histograms of all individuals of *Rhepoxynius abronius* in ten grabs. Shaded areas denote ovigerous females.

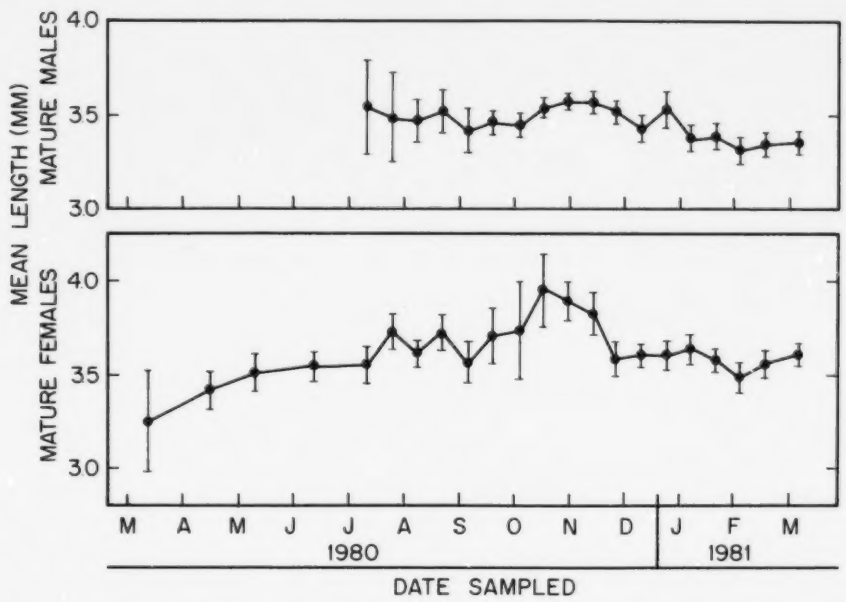

Fig. 2. Mean lengths of mature male and mature female *Rhepoxynius abronius* versus sampling date. Vertical bars are 95% confidence limits.

became bimodal again in late January to March 1981, as small individuals appeared in increasing numbers.

Size at Maturity

All mature females and virtually all mature males (97%) were ≥2.7 mm in length. The annual mean size of mature specimens was 3.47 mm ($N = 897$, $s = 0.28$) for males and 3.60 mm ($N = 1{,}372$, $s = 0.37$) for females. The mean size of mature males was relatively constant through time. Mean size of mature females varied from 3.35 mm in March 1980 to 3.98 mm in October 1980 (Fig. 2).

Reproduction

Reproductive activity as indicated by the number of ovigerous females was minimal in September and October 1980 (Fig. 3a). The number of ovigerous females began to increase in late October, three months prior to the arrival of new recruits in January (Fig. 1), suggesting a time of egg development of approximately three months in fall and early winter. The number of mature males also showed a strong seasonal fluctuation that was not synchronous with that of ovigerous females (Fig. 3b). Mature males were abundant from 11 March to 9 May 1980 and from 18 September 1980 through the end of sampling on 5 March 1981. They were uncommon in July and August, when large numbers of immature males were present. The number of mature males thus increased two months prior to the increase in the number of ovigerous females (Fig. 3a, b), was high during most of the period when ovigerous females were abundant, and decreased

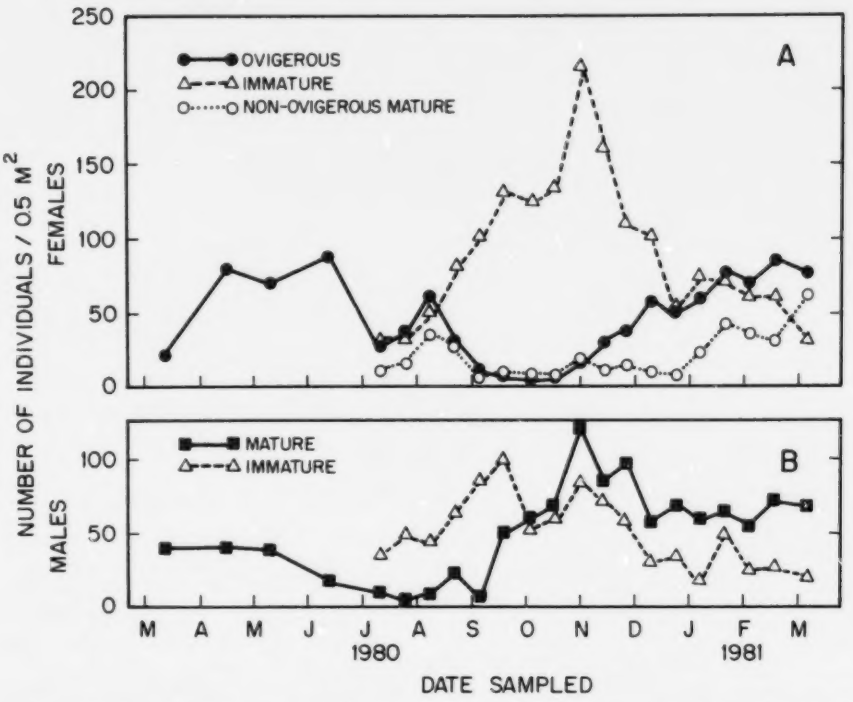

Fig. 3. Abundance of male and female *Rhepoxynius abronius* versus sampling date. Individuals pooled from ten grabs.

two months prior to the decrease in number of ovigerous females. The sex ratio of individuals ≥2.7 mm approached unity in September through early December 1980, when the population was dominated by the young-of-the-year (Fig. 4). The sex ratio favored females in spring through summer 1980 and in spring 1981. Nonovigerous mature females increased in abundance in January 1981, following the increase in number of ovigerous females (Fig. 3a) and concurrent with the onset of recruitment (cf. Fig. 1), indicating that these were females that had recently released their broods. Few of the immature females present after October were greater than 3.2 mm in length; most larger females during the breeding season were ovigerous or had recently released a brood.

The number of eggs per female was averaged for each 0.3-mm size interval over all sampling dates (Fig. 5a). Mean fecundity ranged from about 4 eggs for females less than 3.0 mm in length, to more than 16 eggs for females greater than 4.5 mm in length, averaging 9.3 eggs/female over all size classes. When averaged over sizes within each sampling date, fecundity varied from a minimum of 6.2 eggs/female in early September 1980, to a maximum of 12.9 eggs/female in late October 1980 (Fig. 5b). Based on the curvilinear appearance of the plot of mean fecundity versus length, a power function was used to describe the regression of the number of eggs per brood on length (mm) for all ovigerous females collected:

$$\text{eggs/brood} = 0.340(\text{female length})^{2.485}, \qquad r^2 = 0.21,\ N = 1{,}007.$$

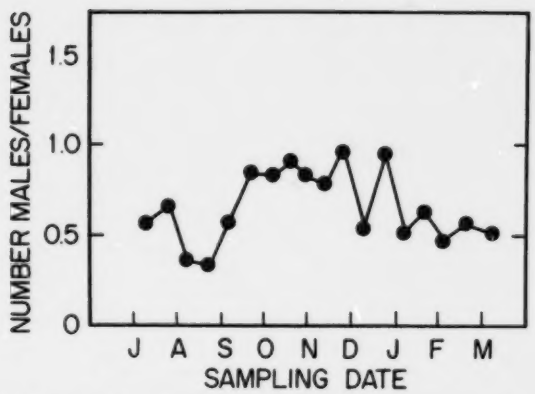

Fig. 4. Ratio of number of male to female *Rhepoxynius abronius* versus sampling date.

Growth and Maturation

An indication of the growth rate of smaller juveniles may be derived from the size-frequency histograms (Fig. 1). The recruit cohort was distinct from the size group representing adults through 11 June 1980. The advance in length of the leading edge of the recruit cohort during this period indicates growth at the rate of one size class, or 0.3 mm, per month. This rate may apply only to the growth of very small individuals. An estimate of the growth of individuals in larger size classes was obtained by grouping all individuals into three size categories: ≤1.1 mm, 1.2–2.6 mm, and ≥2.7 mm. The smallest category represents newly arrived recruits. Growth into the ≥2.7-mm size group corresponds to entry into the size classes in which sexual maturation occurs. The increasing number in the ≥2.7-mm size group five to six months after the onset of recruitment (Fig. 6: 7 August and thereafter) indicates that growth continues at 0.3 mm/month for at least five to six months.

If this growth rate continues to maturation, entry into the ≥2.7-mm size class should be closely followed by maturation as young-of-the-year approach the mean size of mature individuals. This is seen in the increasing number of mature males in September 1980 (Fig. 3b) and the increasing number of mature females in late October 1980 (Fig. 3a). The later maturation of females may reflect their larger size (Fig. 2), or reproductive timing which ensures that mature males are abundant when females undergo the pubertal molt.

Mean size did not change from late October through December, when few recruits were present (Fig. 1: 30 October, mean = 2.60 mm, $s = 0.85$, $N = 949$; 23 December, mean = 2.58 mm, $s = 0.86$, $N = 444$). The size-frequency histograms also show little evidence of adult growth following the arrival of recruits through the end of sampling in March 1981. Recruits arriving in January 1981 also did not grow substantially until early March. Growth in length appears to be minimal from midfall through midwinter.

Biomass

Biomass was estimated from length–frequency data using the equations relating dry weight and ash-free dry weight (AFDW) to length (mm). The equation relating

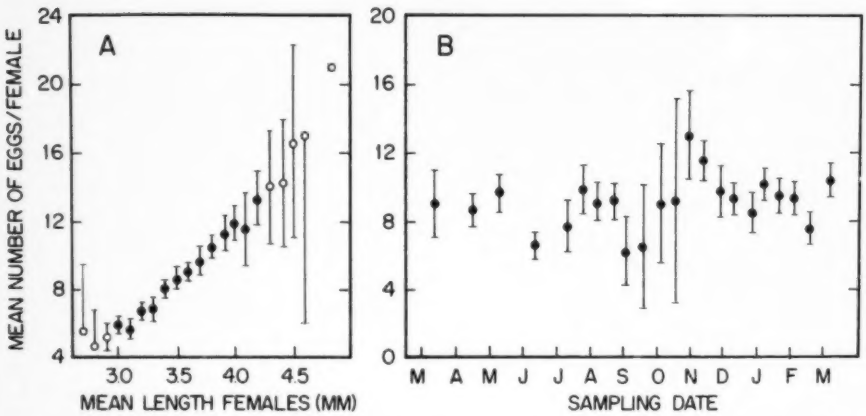

Fig. 5. *Rhepoxynius abronius*. Mean fecundity versus (A) mean female length, (B) sampling date. Vertical bars are 95% confidence limits; one side of limits shown for some points. O = less than 20 females.

wet weight to length may be of value to other studies of phoxocephalids and is also provided:

$$\text{mg wet weight} = 0.0614(\text{length})^{3.373}, \quad r^2 = 0.987,$$
$$\text{mg dry weight} = 0.0186(\text{length})^{3.164}, \quad r^2 = 0.986,$$
$$\text{mg AFDW} = 0.0226(\text{length})^{2.122}, \quad r^2 = 0.967.$$

Biomass (AFDW) ranged from 40 mg/0.5 m^2 on 11 March 1980 to 180 mg/0.5 m^2 on 30 October 1980, averaging 104 mg AFDW/0.5 m^2. On a dry weight basis, biomass ranged from 101 mg/0.5 m^2 to 496 mg/0.5 m^2 on the same dates, averaging 256 mg/0.5 m^2.

Discussion

Recruitment

Recruitment began in March 1980 and in late January 1981, indicating substantial annual variability in timing of life cycle events. The total annual number of recruits can be estimated for 1980 using information on growth rate and the number of individuals in the smallest size class (≤1.1 mm). The estimated growth rate of 0.3 mm/month means that most recruits grow out of the ≤1.1-mm size class in one month. The number of individuals in the ≤1.1-mm size class is therefore an estimate of the number of new recruits which have arrived in the previous month. The sum of the number of recruits in the ≤1.1-mm size class in samples taken at monthly intervals over one year is an estimate of the total annual recruitment/0.5 m^2. This estimate is likely to be low because of mortality occurring between brood release and subsequent sampling. Recruitment averaged 200 recruits/0.5 m^2 per month from March through August 1980, declining to 100 recruits/0.5 m^2 per month in September and to a low of 25 recruits/0.5 m^2 per month from 30 October through December 1980 (Fig. 6). Total annual recruitment in 1980 estimated by this method was approximately 1,300 recruits/0.5 m^2. This estimate should not be greatly biased by cessation of growth in the fall, because few recruits were present.

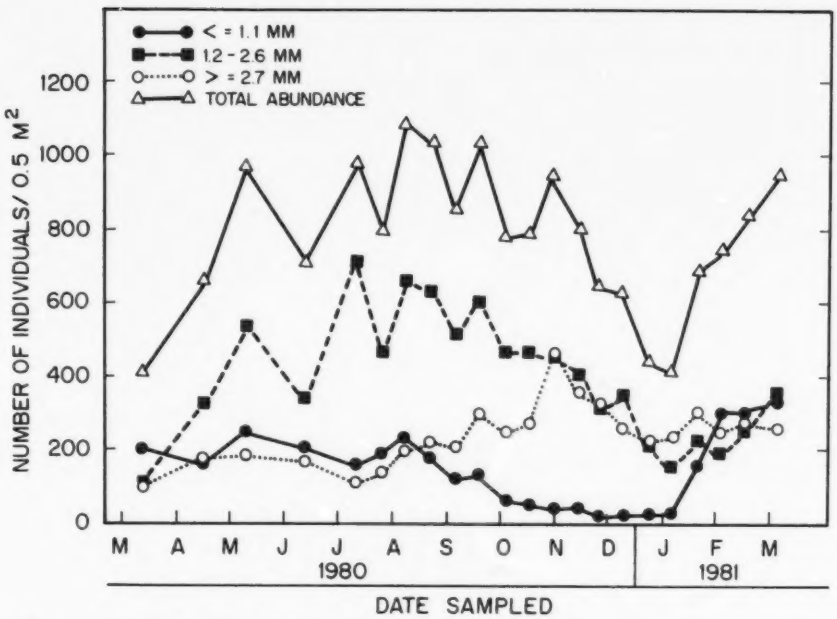

Fig. 6. *Rhepoxynius abronius.* Total abundance and abundance in three size groups versus sampling date. Individuals pooled from ten grabs.

Seasonality of Growth Rate

Indirect evidence suggests that the cessation of growth of adults in midfall may be linked to reproduction. After midfall, a large percentage of females becomes ovigerous and ceases molting. The relatively constant mean size of mature males suggests that males die or stop growing after maturation and reproduction. Energy which was used for increase in body length may be diverted to reproductive effort at this time. Thus, maturation and brood production contribute to the cessation of growth of adults observed in the length–frequency histograms. Since juveniles appeared in January 1981 but apparently did not grow until March 1981, it is likely that other factors contribute to the slow (or zero) winter growth in juveniles or both juveniles and adults.

Reduced growth is probably not due to lower winter temperatures, as observed in other amphipod species (e.g., Hughes, 1982), since summer temperature minima associated with nearshore upwelling did not result in lower growth rates. Other possible causes of slow winter growth include reductions in food supply and stress induced by decreased salinity. The primary food resource of *R. abronius* is unknown, although recent studies indicate that diatoms, larval polychaetes, and nematode meiofauna are ingested (Oliver *et al.*, 1982). Riznyk (1969) observed little or no seasonal variation in diatom abundance near our study site. However, other food resources, including larval polychaetes and meiofauna, may vary in abundance. Swartz *et al.* (1985) reported that salinities less than 25% are acutely toxic to *R. abronius.* Bottom water salinities <25‰ occur infrequently in lower Yaquina Bay. Osmoregulatory stress may therefore limit the distribution of *R. abronius* in Yaquina Bay and may also affect growth at our study site.

Mortality

Independent seasonal estimates of mortality were obtained for 1980–1981. Following an initial increase, the average total number of individuals was about 900/0.5 m^2 from 15 April to 5 September 1980 (Fig. 6). At the same time, new recruits entered the population at a rate of 200/0.5 m^2 per month. Assuming that the relatively stable population size resulted from equal recruitment and mortality rates, and assuming net migration was negligible, approximately 200 postrecruit individuals/0.5 m^2 per month died during spring and summer 1980. This would equal a mortality rate of approximately 22% per month.

The second estimate of mortality is derived from the postrecruitment period between 30 October and 23 December 1980. The total number of individuals/ 0.5 m^2 decreased by 25.3% per month during this period.

The final estimate pertains to the winter and early spring. In the first several samples, no net change in the number of adults was observed (Fig. 6). Recruits grew into larger size classes without apparent reduction in number per size class, suggesting little mortality (Fig. 1: 11 March, 15 April, and 9 May). Mortality therefore appears to have been low during February through early May 1980. A low mortality rate was also evident in winter 1981. As in 1980, the number of older individuals remained relatively constant (Fig. 1: January to early March 1981). Mortality losses are apparently 20–25% per month between mid to late spring and the end of fall, and are low in winter through early spring.

Mortality of benthic Crustacea is commonly attributed to epibenthic or infaunal predators (Wildish and Peer, 1981; Klein *et al.*, 1975; Moore, 1981; Nelson, 1980). Potential predators of *R. abronius* found in Yaquina Bay include juveniles of the buffalo sculpin *Enophrys bison* (Swartz *et al.*, 1974) and the English sole *Parophrys vetulus* (Swartz *et al.*, 1974; Rosenberg, 1980), which are present after March and migrate out of the estuary in the fall. We have also observed megalopae and first crab instars of the Dungeness crab *Cancer magister* in samples taken as early as March; these leave the estuary in the fall as juveniles (Swartz *et al.*, 1974). In the laboratory, juvenile *P. vetulus* and megalopae and first crab instars of *C. magister* were very effective predators of *R. abronius* which had been allowed to bury themselves in sand before predators were introduced. Ambrose (1984) found that juvenile *C. magister* were also predators of *R. abronius* in the laboratory. The correspondence of changes in the mortality rate of *R. abronius* to the presence of potential predators in the estuary suggests that predation is a major cause of mortality. Although migration may contribute to the observed variations in abundance, there is no evidence that significant net migration of *R. abronius* occurs in Yaquina Bay.

The ratio of males to females was nearly 1:1 in the fall, when the young-of-the-year entered the $\geq$2.7-mm size class, but increasingly favored females as reproductive activity increased in mid to late fall (Fig. 4). Similar seasonal changes in the sex ratio of other amphipods have been attributed to postreproduction senescence and death of males (Hastings, 1981; Sainte-Marie and Brunel, 1983), and to higher predation on males associated with emergence of males from the sediment during the reproductive season (Moore, 1981; Wildish and Peer, 1981). The relatively constant mean size of mature males could result from a terminal pubertal molt but may indicate that males mature and reproduce, then die.

The total loss of individuals in 1980 greatly exceeded the number of adults present at the start of 1980, indicating that mortality is not primarily due to death of postreproductive senescent adults, as observed in some other amphipod species (e.g., Dexter, 1971).

Voltinism and Longevity

Many ovigerous females showed advanced ovarian development, including readily identified large oocytes in females carrying developed young. This indicates that a second brood may be produced each year. This possibility was evaluated by comparing the number of recruits to the probable number of progeny of the females present at the start of sampling. Only the first recruits to arrive in 1980 could have matured before the end of the reproductive season. Recruits are therefore produced by year-old females. An average number of 126 adult females/0.5 m^2 were obtained in initial samples from 11 March to 10 July 1980. These produced an estimated total of 1,300 recruits/0.5 m^2, or an average of 10.3 recruits per female (=1,300 recruits/0.5 m^2/yr per 126 females). This is close to the overall mean fecundity of 9.3 eggs/female, and would indicate that females produce one brood per year. However, if substantial mortality of eggs and embryos occurs during development, the effective fecundity of females may be better represented by the mean of 5.08 fully developed young/female ($s = 2.72$) found in a total of 51 females carrying developed broods. The number of developed young in broods was not related significantly to the length of females (linear regression, $r^2 = 0.066$). The observed reduction in mean brood size from egg to developed young may be due to mortality, emergence of juveniles from the brood pouch, or loss from the brood pouch during sampling and handling. Moore (1981) suggested that sampling artifacts may not be a serious source of error in estimating brood mortality of the amphipods *Corophium bonnellii* and *Lembos websteri*. The estimated 45% brood mortality is among higher values reported for marine amphipods (Moore, 1981), but is presumably not entirely due to a sampling artifact. If brood mortality substantially reduces the effective mean fecundity, then the number of recruits per female in 1980 exceeds the effective fecundity of females, and indicates that many females must produce more than one brood per year.

Few large immature females (greater than 3.2 mm in length), but substantial numbers of large, nonovigerous females with setose oostegites were present during the breeding season. After producing their first brood, females probably produce a second brood rather than molt to a "resting" stage with nonsetose oostegites, as occurs in species of *Gammarus* (Steele and Steele, 1975). The mean length of ovigerous females increases near the end of the breeding season, when few ovigerous females are present. This increase in length may be due to late maturing larger females or to renewed molting of females which have already reproduced.

Lowered fecundity in summer has been described for several amphipod species (e.g., Sameoto, 1969; Dexter, 1971; Fish, 1975), is observed even after correcting for seasonal variations in female size (Nelson, 1980), and may be due to reduced food supply (Fish, 1975) or decreased allocation of energy to reproduction (Mathias, 1971). Summer fecundities observed in this study were not consistently lower than winter fecundities (Fig. 5b), and variations were minor compared to the more than fivefold seasonal variations observed by Nelson (1980).

It is not possible to determine conclusively the maximum life-span of *R. abronius* because of the overlap of year-classes. However, with the observed pattern of mortality, the approximately 150 adults/0.5 m^2 present in the initial samples would have been reduced to only 19 of the 400 individuals/0.5 m^2 present at the end of the year. The reproductive contribution of individuals greater than one year old is probably minor, and for practical purposes this population of *R. abronius* is replaced annually. An annual life history in which females produce one or two broods per lifetime is typical of sublittoral marine amphipods (Wildish and Peer, 1981).

Total Population Abundance

The variation in total abundance through time (Fig. 6) shows the net effects of recruitment, growth, and mortality. Recruitment exceeded mortality in spring 1980, when the total number of individuals increased. Mortality increased in late spring and summer and approximately equaled recruitment, resulting in little net change in total abundance. Recruitment declined in late summer, while mortality continued at about 20–25% per month, resulting in declining total abundance during fall 1980. In January 1981, reduced mortality combined with the arrival of the 1981 recruits increased the population density. By March 1981, the population density had returned to the mid-1980 level. A similar decline and subsequent increase in abundance in fall 1970 and winter 1971 was noted for *Paraphoxus fatigans* in the low intertidal of Yaquina Bay, within 2 km of our study site (Bosworth, 1976). We have found *R. abronius* intertidally at that location, indicating that Bosworth's *P. fatigans* (now *R. fatigans*) may have been the morphologically very similar *R. abronius*. Thus, the seasonal variations in mortality and abundance observed in this study are probably not the result of unusual events peculiar to 1980–1981.

The abrupt decline in total abundance during fall 1980 was not caused by an increase in mortality, but rather by the normal fall decline in recruitment. Increasing mortality in spring 1980 was offset by recruitment, thus stabilizing total abundance. This demonstrates the importance of complete life cycle information to interpret short-term phenomena. In this study, sampling during fall and winter 1980 alone may have led to the incorrect conclusion that an episodic increase in mortality had led to the apparent population crash and subsequent recovery.

Rhepoxynius abronius is found subtidally over a considerable depth range on the continental shelf (Barnard and Barnard, 1982) and penetrates only into the lower Yaquina Bay estuary. The life history of this estuarine population of *R. abronius* is similar to that of an outer coastal population, in having an annual life cycle, overlapping generations, and one or two broods per female (Hannan *et al.*, 1979). The outer coastal population declined in abundance in fall (1971 and 1972), as observed in the estuarine population. This suggests similar timing of seasonal fluctuations in mortality of estuarine and continental shelf populations. The range of body size, mean size of mature females, and range and mean brood fecundity were also similar. However, the number of ovigerous females in the outer coastal population increased after January and the onset of recruitment occurred consistently after March, later than observed for our study population. No data are available to compare growth and mortality rates, or duration of recruitment.

Environmental factors may result in differences in the life history of estuarine and outer coast populations of species such as *R. abronius* that do not migrate extensively. Estuarine populations will undoubtedly be subject to seasonal changes in the abundance of predators, temperature, salinity, and other physical and biological environmental variables which will be different from those experienced by a nonestuarine population. Such nongenetic factors may result in large differences between the characteristic life histories of populations of a given species (Wildish and Peer, 1981, cf. Cederwall, 1977; Sainte-Marie and Brunel, 1983). In the case of *Rhepoxynius abronius,* outer coastal and estuarine populations may differ primarily in the timing of reproductive events. A comparison of the mortality and growth rates of estuarine and outer coastal populations of *R. abronius* would be valuable in determining further the manner and extent to which environmental factors influence the life history of this species.

Productivity

Production of the 1980 recruits through the end of 1980 was calculated for a model population based on the estimated rates of recruitment, growth, and mortality. For computation purposes, groups of recruits arriving at monthly intervals were treated as separate cohorts and their production estimated by a cohort summation-of-losses method (Crisp, 1971). Components of production which were not considered include exuviae and nonviable eggs. Seasonal changes in the length-weight relationship, especially increasing weight per length in the breeding season, were not taken specifically into account. However, much of the weight increase associated with reproduction is ultimately incorporated into progeny and therefore is included in production and biomass estimates. Model assumptions made in estimating production were: (1) Mortality was negligible through 9 May and 22.5% per month thereafter through December, with individuals dying in the middle of the month; (2) Recruitment was constant at 200/0.5 m^2/month from March through August, declining to 100/month in September and to a low of 25/month from 30 October through the remainder of the year; and (3) Growth was constant for all individuals at 0.3 mm/month through 30 October and negligible thereafter. The hypothetical population was thus closely based on the observed population in 1980. However, the parameters used resulted in a predicted total population of 285/0.5 m^2 at the end of 1980, somewhat less than the observed 400/0.5 m^2. This difference was within sampling error in estimating field abundances, and no adjustments in population parameters were made.

Since recruitment and growth (in length) were minor after October 1980, the cohort production in 1980 was estimated as the predicted standing biomass on 30 October (64.2 mg AFDW/0.5 m^2; 143.9 mg dry weight/0.5 m^2) plus the biomass of all individuals that died through 30 October. Production by this method was 160 mg/0.5 m^2 AFDW, or 331 mg/0.5 m^2 dry weight.

This underestimates annual production, because renewed growth of individuals in the spring of the following year was not included and because some growth may have occurred during winter 1980, even though molting was rare. The extent of underestimation was evaluated. The mean size of individuals of the model population at the end of 1980 was 2.2 mm. If all these individuals were to survive and grow to the overall mean adult size of 3.54 mm, the added production of biomass would be 56 mg AFDW/0.5 m^2 or 203 mg dry weight/0.5 m^2. Annual production is therefore 160–216 mg AFDW/0.5 m^2 or 331–534 mg dry weight/0.5 m^2. Since the model population was smaller at the end of 1980 than the real population and some components of production were not evaluated, this should be considered a minimum production estimate. The ratio of estimated production to observed mean biomass was 1.54–2.08 for AFDW and 1.29–2.09 for dry weight. The two P:B estimates are not identical because the corresponding production values were calculated independently.

With the exception of amphipods of the brackish-water Black Sea (see Zaika, 1973), most estimates of production in marine amphipods have been for ampeliscid, pontoporeid, and corophiid amphipods (Table 1). Secondary production estimated for the phoxocephalid amphipod *Harpinia propinqua* was 66 mg wet weight/m^2/yr, with a production to biomass ratio of 3.14–3.77 (Wildish, 1984). An approximate wet weight to dry weight conversion factor of 25% (from *R. abronius* equations) yields an estimated production of 16.5 mg dry weight/m^2/yr for *H. propinqua*. Thus, biomass-specific production is greater for *H. propinqua* than for *R. abronius*, but the higher density of *R. abronius* in Yaquina Bay results

Table 1. Secondary production estimates for marine amphipods. P = production (grams/m²/yr); B = biomass (grams/m²); P:B = production/biomass; G = generation/yr. Weight units are: * = dry weight; ** = ash-free dry weight; *** = wet weight; **** = carbon weight. + = calculated over four months; ++ = P in grams/m²/day, P:B in day⁻¹; +++ = preserved wet weight.

Species	P		B	P:B	G	Source
Ampelisca spinipes	0.18	*	0.07	2.4	1	Glemarac and Menesguen, 1980
araucana	8.03–12.43	*	1.88–2.20	3.65–4.45	2	Carrasco and Arcos, 1984
brevicornis	0.30–0.70	*	0.10–0.20	3.40–4.40	1	Klein *et al.*, 1975
brevicornis	1.31–1.68	*	0.52	2.49–3.21	1	Hastings, 1981
tenuicornis	0.10	**	0.03	3.4	1	Sheader, 1977
Haploops fundiensis	1.0	***+++	0.78	1.29	0.5	Wildish, 1984
Pontoporeia affinis	1.92–4.42	*	1.62–1.70	1.19–2.60	0.5	Cederwall, 1977
femorata	1.44–4.63	*	1.84–2.22	0.78–2.08	0.5	Cederwall, 1977
femorata	11.06–13.61	***	2.40–3.73	3.64–4.78	1	Wildish and Peer, 1981
Urothoe brevicornis	1.33–1.89	*	—	0.94–1.58	0.5	Hastings, 1980; in Hastings, 1981
Corophium salmonis	3.62–10.72	*	0.42–1.30	7.20–8.60	several	Albright and Armstrong, 1982
insidiosum	3.0–60.00	*	—	12.0–19.5	several	Casabianca, 1975; in Birklund, 1977
insidiosum	0.23–8.37	*+	0.08–1.70	3.0–4.9	several	Birklund, 1977
volutator	2.46–3.79	*+	0.56–1.19	3.2–4.4	several	Birklund, 1977
volutator	13.4	****	1.9	7.0	several	Mossman, 1978; in Carrasco and Arcos, 1984
Talorchestia margaritae	1.81	*++	21.74	0.08	several	Venables, 1981
Photis reinhardi	0.74	***+++	0.27	2.78	2	Wildish, 1984
Casco bigelowi	1.21	***+++	0.49	2.46	1	Wildish, 1984
Haustorius canadensis	1.02	**	0.69	1.48	0.5	Donn and Croker, 1983
Harpinia propinqua	0.066	***+++	0.021	3.14	1	Wildish, 1984
Rhepoxynius abronius	0.66–1.07	*	0.51	1.29–2.09	1	this study
abronius	0.32–0.43	**	0.21	1.52–2.08	1	this study

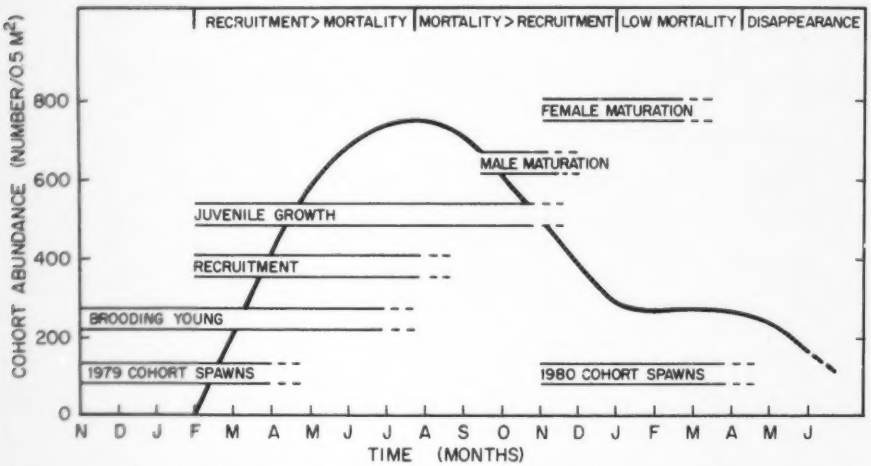

Fig. 7. Life history and abundance of a single cohort of *Rhepoxynius abronius*. Solid horizontal lines denote peak activity, dashed lines declining activity. Abundance predicted for a model population. Spawning refers to release of eggs into brood pouch.

in a much higher total annual production per unit area. Production and the P:B ratio of *R. abronius* are within the lower range of reported values for other marine amphipods but are similar to those of marine amphipods producing one or fewer generations per year (Table 1).

Life Cycle Summary

The timing and duration of major life history events, as experienced by most members of a cohort, are summarized in Fig. 7. Eggs are spawned and brooded in late fall through spring, with release of the young-of-the-year in the winter through most of the summer. Maturation of the young-of-the-year occurs in fall and winter, with males maturing earlier than females. Although the life-span of an individual is unknown, the cohort as a whole persists for approximately 18 months. Seasonal variations in the total population density result from predictable fluctuations in recruitment and mortality rates.

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